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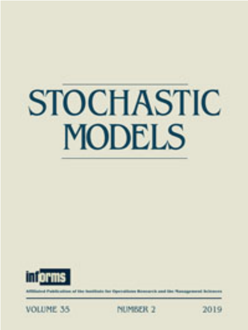

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Populations with interaction and environmental dependence: From few, (almost) independent, members into deterministic evolution of high densities

Pavel Chigansky[a], Peter Jagers[b], and Fima C. Klebaner[c]

[a]Department of Statistics, The Hebrew University, Jerusalem, Israel; [b]Department of Mathematical Sciences, Chalmers and the University of Gothenburg, Gothenburg, Sweden; [c]School of Mathematical Sciences, Monash University, Melbourne, VIC, Australia

ABSTRACT

Many populations, e.g. not only of cells, bacteria, viruses, or replicating DNA molecules, but also of species invading a habitat, or physical systems of elements generating new elements, start small, from a few Individuals, and grow large into a noticeable fraction of the environmental carrying capacity K or some corresponding regulating or system scale unit. Typically, the elements of the initiating, sparse set will not be hampering each other and their number will grow from $Z_0 = z_0$ in a branching process or Malthusian like, roughly exponential fashion, $Z_t \sim a^t W$, where Z_t is the size at discrete time $t \to \infty$, $a > 1$ is the offspring mean per individual (at the low starting density of elements, and large K), and W a sum of z_0 i.i.d. random variables. It will, thus, become detectable (i.e. of the same order as K) only after around log K generations, when its density $X_t := Z_t/K$ will tend to be strictly positive. Typically, this entity will be random, even if the very beginning was not at all stochastic, as indicated by lower case z_0, due to variations during the early development. However, from that time onwards, law of large numbers effects will render the process deterministic, though inititiated by the random density at time log K, expressed through the variable W. Thus, W acts both as a random veil concealing the start and a stochastic initial value for later, deterministic population density development. We make such arguments precise, studying general density and also system-size dependent, processes, as $K \to \infty$. As an intrinsic size parameter, K may also be chosen to be the time unit. The fundamental ideas are to couple the initial system to a branching process and to show that late densities develop very much like iterates of a conditional expectation operator. The "random veil", hiding the start, was first observed in the very concrete special case of finding the initial copy number in quantitative PCR under Michaelis-Menten enzyme kinetics, where the initial individual replication variance is nil if and only if the efficiency is one, i.e. all molecules replicate.

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CONTACT Peter Jagers jagers@chalmers.se Department of Mathematical Sciences, Chalmers and the University of Gothenburg, Gothenburg, Sweden

1. Introduction: Replication with interaction and dependence

We consider sets of elements where, in principle, each element may generate new elements. For lucidity we regard time as discrete, labeling it by $n = 0, 1, 2, \ldots$, referring to it also as generations, cycles or rounds, and call the system a 'population' of 'individuals', even though we have quite general such structures in mind. This is like in branching processes,[5,6] but without independence between individuals required. Here, we assume that the individual offspring generation (reproduction, replication or whatever) may be influenced by a system 'carrying capacity', K, which we think of as large, as compared to the population starting number Z_0, and also by the number of other individuals present. We say that replication is capacity and population size, or 'density' dependent, as in Refs. [1,2].

The process definition is patterned after the recursive scheme used to build up Galton–Watson processes: Let

$$\xi_{n,j}, n \in \mathbb{N}, j \in \mathbb{N},$$

be non-negative integer-valued random variables, where we think of $\xi_{n,1}, \xi_{n,2}, \ldots$ as the possible offspring numbers of various individuals in the n – 1:th generation. Thus, we define $\{Z_n, n = 0, 1, 2, \ldots\}$, by the initial number Z_0 and

$$Z_n = \sum_{j=1}^{Z_{n-1}} \xi_{n,j}. \tag{1.1}$$

The dependence structure is made precise in a basic assumption:

(A0) For each fixed $n \in \mathbb{N}$, the $\xi_{n,j}, j = 1, 2, \ldots$, are *conditionally* independently and identically distributed, given the preceding, $\mathcal{F}_{n-1} := \sigma(\{\xi_{k,j}, k<n, j \in \mathbb{N}\})$. The process is Markovian in the sense that the conditional distribution should be determined by the couple K and $X_{n-1} = Z_{n-1}/K$, the *carrying capacity* and *population density*, in such a manner that the variables $\xi_{k,j}$ increase in distribution with K and decrease with $x = X_{n-1}$, the limiting distribution, as $K \to \infty$, *the asymptotic reproduction*, being proper for each $x \in \mathbb{R}_+$.

Three entities pertaining to the density turn out to be crucial for the analysis of process start and late development. They are:

1. the conditional mean number of offspring per individual,

$$m^K(X_{n-1}) = \mathbb{E}\left[\xi_{n,i} | \mathcal{F}_{n-1}\right],$$

2. the corresponding variance,

$$\sigma_K^2(X_{n-1}) = \mathrm{Var}\left[\xi_{n,i} | \mathcal{F}_{n-1}\right],$$

3. and the conditional expectation of the density process,

$$f^K(x) = \mathbb{E}[X_n | X_{n-1} = x] = xm^K(x),$$

where the dependence of variance and expectation operators upon K is implicit. From A0, it follows that the m^K form za non-decreasing sequence of non-increasing functions, and hence must have a non-increasing limit, m. The means and variances m^K and σ_K^2 are supposed defined on all of $\mathbb{R}_+$.

We formulate boundedness and smoothness criteria for these functions, which will lead to classical Malthusian growth for Z_n in an early stage, $n \le n_K = c \log K, 0<c<1$. Then, we make use of a law of large numbers for branching processes with a threshold and density dependence,[8] and a large initial value, in our case $O(K^c)$, at round n_K. All logarithms are with base a.

The assumptions beyond A0 are:

(A1) The limiting expected conditional reproduction given a population density x, $m(x)$ has a derivative which is uniformly continuous in a neighbourhood to the right of the origin, and $a = m(0) > 1$. As $K \to \infty$, the continuous non-increasing functions m^K converge uniformly to a bounded differentiable function m, $0 \le m(x) - m^K(x) \le Cx + o(x)$ for some $C > 0$ and uniformly in K, as $x \to 0$.

(A2) The limiting conditional expected density $f, f(x) = xm(x), x \ge 0$, is strictly increasing.

(A3) As $K \to \infty$, X_0 converges in probability to some limit $x_0 \ge 0$. In particular, if there is a fixed starting number, $x_0 = 0$.

(A4) The conditional reproduction variance $\sigma_K^2(x) = \mathrm{Var}[\xi_{n,i} | X_{n-1} = x]$ is uniformly bounded and, as $K \to \infty$, converges to some $\sigma^2(x)$ uniformly. The latter, hence, is also bounded.

(A5) There is a constant $C > 0$ such that uniformly for all K

$$a \ge m^K(x) = m^K(0) - Cx + o(x) \quad \text{as} x \to 0.$$

Further, $0 \le a - m^K(0) = O(1/\sqrt{K})$ and also $\sup_{x \ge 0} |f^K(x) - f(x)| = O(1/\sqrt{K})$.

These look like innocuous smoothness requirements, but A2 contains something more. For fixed K dependence upon the density is the same as dependence on population size, and it thus seems little of a restriction to ask that the next generation should tend to increase with density. It might however be argued that there could be a density above which for example no replication is possible. This in a sense, however, would introduce a sort of further carrying capacity, besides K.

2. In spite of interaction and capacity dependence, the beginning looks like branching, when the carrying capacity becomes large

An approximating process, at low density and high carrying capacity, $\tilde{Z} = \{\tilde{Z}_n\}$, is crucial in the analysis. It has the same starting number $Z_0 = z_0$ as the original process, but then it continues as a classical Galton–Watson process,

$$\tilde{Z}_0 = z_0 \tag{2.1}$$

$$\tilde{Z}_n = \sum_{j=1}^{\tilde{Z}_{n-1}} \eta_{n,j}, \tag{2.2}$$

where the η variables are i.i.d. with the asymptotic reproduction distribution as $K \to \infty$ for $x=0$. Thus, $\mathbb{E}[\eta] = a = m(0)>1$ and $\mathrm{Var}[\eta] = \sigma^2(0)<\infty$.(Lower case z_0 indicates an unknown but deterministic starting number.)

From classical branching process theory, $W(z_0) := \lim_{n\to\infty} \tilde{Z}_n/a^n$ will have the distribution of z_0 independent W-copies, each with expectation 1 and variance $\sigma^2(0)/(a^2-a)$. In particular,

$$\tilde{Z}_{n_K}/K^c = \tilde{Z}_{n_K}/a^{n_K}\sim W(z_0).$$

By approximation, this extends to:

Theorem 2.1. *Under assumptions A0, A1, and A5, $Z_{n_K}/a^{n_K} \to W(z_0)$ and thus $X_{n_K}\sim W(z_0)K^{c-1}$, in probability and L^1, as $K \to \infty$.*

Proof. Construct the replication processes Z and $\tilde{Z}$, as well as a third process $Z^\gamma = \{Z_n^\gamma\}$, on the same probability space by the following coupling. Let $U_{n,j}, n, j \in \mathbb{N}$ be independent uniformly distributed random variables on [0, 1]. For each K and x define $t_{-1}^K(x) = t_{-1} = 0$ and $0 \le t_0^K(x) \le t_1^K(x) \le t_2^K(x) \le \dots$ so that $\mathbb{P}(t_{k-1}^K(x)<U_{n,j} \le t_k^K(x)) = \mathbb{P}(\xi_{n,j} = k|X_{n-1} = x), k \in \mathbb{N}$. Further, let $0 \le t_0 \le t_1 \le t_2 \le \dots$ so that $\mathbb{P}(t_{k-1}<U_{n,j} \le t_k) = \mathbb{P}(\eta_{n,j} = k), k \in \mathbb{N}$. We can then define the reproduction random variables $\xi_{n,j}$ and population sizes Z_n, $\tilde{Z}_n$, as well as densities X_n inductively on the same probability space by,

$$\xi_{n,j} = k \Longleftrightarrow t_{k-1}^K(X_{n-1})<U_{n,j} \le t_k^K(X_{n-1}) \text{ and } \eta_{n,j} = k \Longleftrightarrow t_{k-1}<U_{n,j} \le t_k.$$

and, as before, (1.1) and (2.1), using $\xi_{n,j}$ and $\eta_{n,j}$ respectively. Similarly, we write

$$\xi_{n,j}^\gamma := \sum_{k=0}^{\infty} k 1_{\left(t_{k-1}^K(K^{\gamma-1}), t_k^K(K^{\gamma-1})\right]}(U_{n,j})$$

and Z_n^γ correspondingly.

By the distributional properties of $\xi_{n,j}|X_{n-1} = x$ and $\eta_{n,j}$ (Assumption A0),

$$t_k^K(x) = \mathbb{P}\big(\xi_{n,j} \le k|X_{n-1} = x\big) \ge \mathbb{P}\big(\eta_{n,j} \le k\big) = t_k$$

and

$$t_k^K(K^{\gamma-1}) \ge t_k^K(X_n),$$

the latter as long as $n<\tau := \inf\{n; X_n>K^{\gamma-1}\}$. Hence, by induction for the random entities realized with the help of the $U_{n,j}, \tilde{Z}_n \ge Z_n, n \in \mathbb{N}$, pointwise, and $Z_n^\gamma \le Z_n, n<\tau$. Further, $\tilde{Z}_n \ge Z_n^\gamma$ for all n. It follows that

$$0 \le \tilde{Z}_n - Z_n \le \tilde{Z}_n - Z_n^\gamma 1_{\{n<\tau\}} - Z_n 1_{\{n\ge\tau\}} \le \tilde{Z}_n - Z_n^\gamma 1_{\{n<\tau\}} \le \tilde{Z}_n - Z_n^\gamma + Z_n^\gamma 1_{\{n\ge\tau\}}.$$

Now, in order to show that

$$\lim_{K\to\infty} \big(\tilde{Z}_{n_K} - Z_{n_K}\big)K^{-c} = 0,$$

we choose $1/2 < c < \gamma < 1$. By this and A5,

$$\begin{aligned} a \ge m^K(K^{\gamma-1}) = {} & a - \big(a - m^K(0)\big) - \big(m^K(0) - m^K(K^{\gamma-1})\big) \ge \\ & a - aAK^{-1/2} - aBK^{\gamma-1} + o(K^{\gamma-1}) = a(1 - BK^{\gamma-1} + o(K^{\gamma-1})) \end{aligned}$$

for suitable constants A and B.

Hence,

$$\begin{aligned} \mathbb{E}\Big(\tilde{Z}_{n_K} - Z_{n_K}^\gamma\Big) = {} & z_0\big(a^{n_K} - m^K(K^{\gamma-1})^{n_K}\big) = \\ z_0 a^{c\log K}\Big(1 - (1 - BK^{\gamma-1} + o(K^{\gamma-1}))^{c\log K}\Big) & = o(K^c). \end{aligned}$$

Thus,

$$\mathbb{E}\Big[\tilde{X}_{n_K} - X_{n_K}^\gamma\Big] = o(K^{c-1}).$$

For the remaining term, note that

$$\mathbb{E}\big[Z_{n_K}^\gamma; \tau \le n_K\big] \le \mathbb{E}\big[\tilde{Z}_{n_K}; \tau \le n_K\big] \le \Big(\mathbb{E}\Big[\tilde{Z}_{n_K}^2\Big]\mathbb{P}(\tau \le n_K)\Big)^{1/2},$$

by the Cauchy-Schwartz inequality. Since $Z_n \le \tilde{Z}_n$ for all n, it takes longer for the former process to reach K^γ than for the latter, so that

$$\tau \ge \nu := \inf\{n : \tilde{Z}_n > K^\gamma\}$$

and

$$\begin{aligned} \mathbb{P}(\tau \le n_K) \le {} & \mathbb{P}(\nu \le n_K) = \mathbb{P}\Big(\sup_{n\le n_K} \tilde{Z}_n > K^\gamma\Big) = \\ & \mathbb{P}\Big(a^{-n_K}\sup_{n\le n_K} \tilde{Z}_n > K^\gamma a^{-n_K}\Big) \le \\ & \mathbb{P}\Big(\sup_{n\le n_K} \tilde{Z}_n a^{-n} > K^{\gamma-c}\Big) \le K^{c-\gamma}, \end{aligned}$$

where the last bound is Doob's inequality for the martingale $\{\tilde{Z}_n a^{-n}\}$. Since $\mathbb{E}[\tilde{Z}^2_{n_K}] = O(K^{2c})$, by the formula for expectation and variance of Galton–Watson processes,

$$\lim_{K\to\infty} K^{-c}\mathbb{E}\left[\tilde{Z}_{n_K}; \nu \le n_K\right] = 0.$$

Recalling that $\gamma > c$, we conclude that

$$\lim_{K\to\infty} \left(\tilde{Z}_{n_K} - Z_{n_K}\right)K^{-c} = 0. \tag{2.3}$$

holds in L^1, and hence in probability. For the corresponding densities, division by K yields

$$\lim_{K\to\infty} \left(\tilde{X}_{n_K} - X_{n_K}\right)K^{1-c} = 0.$$

3. The branching like stage forms a random initial condition for later development

If the process does not die out, it will thus grow exponentially in n, at least as long as it does not approach K and for fixed K this holds for some $n_K = c\log K$ generations. Then, law of large numbers type effects should stabilize the subsequent growth. We proceed to this, giving first a result on densities for fixed time, $K \to \infty$, and K-dependent but stabilizing starting density X_0:

Theorem 3.1. *Under the assumptions stated, for any time n,*

$$\lim_{K\to\infty} X_n = x_n,$$

in probability, where x_n is the n:th iterate of f, $x_n = f_n(x_0)$. If $X_0 \to x_0$ holds in L^1, the conclusion can actually be strengthened to mean square convergence.

For a proof (under somewhat weaker conditions), see Ref. [10], or Theorem 1 of [8].

Now, in our framework the second, "post-branching", stage starts at time n_K from $W(z_0)a^{n_K} = W(z_0)K^c$ individuals. Hence, the starting density, $W(z_0)K^{c-1} \to x_0 = 0$. But this is a fixed point of f, and so Theorem 3.1 just yields convergence to zero. The remedy is to consider ever later time points.

Lemma 3.2. *If f increases strictly but m decreases and $a = m(0) > 1$ (Assumptions A0, A1, and A2), then*

$$h(x) = \lim_{n\to\infty} f_n(x/a^n).$$

is well defined, continuous, and strictly increasing. The convergence is uniform and $h(0) = 0$.

Proof. Since f is increasing, so are all f_n. By definition,

$$f(x/a) = m(x/a)x/a \leq m(0)x/a = x,$$

for $x \geq 0$. Hence,

$$f_{n+1}\left(x/a^{n+1}\right) = f_n\left(f\left(x/a^{n+1}\right)\right) \leq f_n(x/a^n).$$

The sequence $h_n(x) := f_n(x/a^n)$ thus decreases in n for any positive x, and its limit h, as $n \to \infty$, must exist and be a non-decreasing function, like the f_n. By Dini's theorem, the convergence is uniform on any compact interval. Clearly, $h(0) = h_n(0) = f_n(0) = 0$ for all n.

It remains to prove that the limit h increases strictly. However, there exist $C > 0$ and $\epsilon > 0$ such that

$$f'(x) = m(x) + xm'(x) = m(0) + m(x) - m(0)$$
$$+ xm'(x) \geq a - 2x \sup_{0 \leq u \leq x} |m'(u)| > a - Cx > 0,$$

for $0 < x < \epsilon$. For any $x < \min(\epsilon, 1/C)$,

$$h'_n(x) = a^{-n} f'_n(x/a^n) = a^{-n} \prod_{j=0}^{n-1} f'\left(f_j(x/a^n)\right) \geq a^{-n} \prod_{j=0}^{n-1}\left(a - Cf_j(x/a^n)\right) \geq$$
$$a^{-n} \prod_{j=0}^{n-1}\left(a - Cxa^{j-n}\right) \geq \prod_{j=0}^{n-1}\left(1 - a^{-j}\right) \geq e^{-a}, \quad \forall\ n \geq 0.$$

Taking the limit $n \to \infty$, we see that h increases strictly in an open neighborhood of the origin. However, as $f_{n+1}(x/a^{n+1}) = f(f_n((x/a)/a^n))$, letting $n \to \infty$, shows that h solves Schröder's functional equation

$$h(x) = f(h(x/a)).$$

Therefore, if it were constant on an interval $[x_1, x_2]$ with $x_2 > x_1$, then also $h(x_1/a^k) = h(x_2/a^k)$, for any integer $k \geq 1$, contradicting the fact that h increases strictly on some neighborhood of the origin. Thus, h must be strictly increasing on the positive half line. □

An immediate consequence of this will be of explicit use in the proof of our main Theorem 3.6 later:

Corollary 3.3.

$$\lim_{n\to\infty} f_n\left(x/a^n + o\left(a^{-n}\right)\right) = h(x). \tag{3.1}$$

Now, for fixed K, the density process X satisfies the fundamental recursive equation (cf. [8])

$$X_n = f^K(X_{n-1}) + \frac{1}{\sqrt{K}} \varepsilon_n, \tag{3.2}$$

where

$$\varepsilon_n = \frac{1}{\sqrt{K}} \sum_{j=1}^{KX_{n-1}} \left(\xi_{n,j} - \mathbb{E}\left[\xi_{n,j} | \mathcal{F}_{n-1}\right]\right)$$

a martingale difference sequence, $\mathbb{E}[\varepsilon_n | \mathcal{F}_{n-1}] = 0$, with

$$\mathbb{E}\left[\varepsilon_n^2 | \mathcal{F}_{n-1}\right] = \mathrm{Var}[\varepsilon_n | \mathcal{F}_{n-1}] = \sigma_K^2(X_{n-1}).$$

The corresponding deterministic recursion, obtained by omitting the martingale difference term, is

$$x_n^K = f^K\left(x_{n-1}^K\right) = f_n^K(x_0).$$

From now on, what is needed of Assumptions A0-A5 is used freely. We take $1/2 < c < 1$, write $\nu_K = \log K - n_K = (1-c)\log K$, and interpret X subscripts as their integral parts.

Lemma 3.4.

$$X_{\log K} - f_{\nu_K}^K(X_{n_K}) \xrightarrow[K\to\infty]{L^1} 0.$$

Proof. Write

$$\Delta_n = X_n - f_{n-n_K}^K(X_{n_K}),$$

for $n > n_K$. Then,

$$\Delta_n = f^K(X_{n-1}) + \frac{1}{\sqrt{K}}\varepsilon_n - f^K \circ f_{n-1-n_K}^K(X_{n_K}).$$

Since for any $x \geq 0, 0 \leq \frac{d}{dx} f^K(x) = m^K(x) + x\frac{d}{dx} m^K(x) \leq m^K(x) \leq a$ by assumption,

$$|\Delta_n| \leq |f^K(X_{n-1}) - f^K \circ f_{n-1-n_K}^K(X_{n_K})| + |\frac{1}{\sqrt{K}}\varepsilon_n| \leq$$

$$a|\Delta_{n-1}| + |\frac{1}{\sqrt{K}}\varepsilon_n| \leq \ldots \leq \sum_{j=0}^{n-n_K-1} a^j |\frac{1}{\sqrt{K}}\varepsilon_{n-j}|.$$

Adding to this that, for any natural k,

$$\mathbb{E}\left[|\varepsilon_k| \leq \sqrt{\mathbb{E}\left[\varepsilon_k^2\right]} = \sqrt{\mathbb{E}\left[\mathbb{E}\left[\varepsilon_k^2 | X_{k-1}\right]\right]}\right] \leq \sup_x \sigma_K(x) < \infty,$$

by A4, we can conclude that

$$\mathbb{E}\left[|\Delta_{\log K}|\right] \leq C a^{\nu_K} \frac{1}{\sqrt{K}} \sup_x \sigma_K(x) = C K^{1/2-c} \sup_x \sigma_K(x) \to 0,$$

as $K \to \infty$. □

Lemma 3.5.

$$f_{\nu_K}^K(X_{n_K}) - f_{\nu_K}(X_{n_K}) \to 0.$$

Proof. By Assumption A5, for any $0 \le x \le 1$ and some $C > 0$,

$$|f_n^K(x) - f_n(x)| \le |f^K \circ f_{n-1}^K(x) - f \circ f_{n-1}^K(x)| + |f \circ f_{n-1}^K(x) - f \circ f_{n-1}(x)| \le$$

$$C/\sqrt{K} + a|f_{n-1}^K(x) - f_{n-1}(x)|.$$

Hence, by induction, for any x and n

$$|f_n^K(x) - f_n(x)| \le \frac{C}{\sqrt{K}} \sum_{j=0}^{n-1} a^j \le \frac{C}{(a-1)\sqrt{K}} a^n,$$

and

$$\sup_{0 \le x} |f_{\nu_K}^K(x) - f_{\nu_K}(x)| = O\left(a^{\nu_K}/\sqrt{K}\right) = O(K^{1/2-c}) \to 0,$$

as $K \to \infty$. □

After these lemmas and the corollary, the proof of the main theorem below is direct.

Theorem 3.6. *Assume $Z_0 = z_0$ given and all of Assumptions A0-A5 valid. Then $X_{\log K}$ converges in distribution*

$$X_{\log K} \xrightarrow[K\to\infty]{D} h \circ W(z_0).$$

Remark 3.7. The limits increase strictly with n. Recall that logarithms are with base a.

Corollary 3.8. *For any fixed n*

$$X_{\log K+n} \xrightarrow[K\to\infty]{D} f_n \circ h \circ W(z_0),$$

where f_n still denotes the n-th iterate of f. This extends to weak convergence of the sequences, regarded as random elements in $\mathbb{R}^{\mathbb{Z}}$:

$$\{X_{\log K+n}\}_{-\infty}^{\infty} \xrightarrow[K\to\infty]{D} \left\{f_n \circ h \circ W((z_0)\right\}_{-\infty}^{\infty}.$$

Proof. This follows by induction on n from the fundamental representation (3.2). For $n = 0$ it is the statement of the main result. For $n = 1$ take limits as $K \to \infty$ in (3.2), and note that the stochastic term vanishes. Similarly, if it holds true for n, it follows for $n+1$. Functional convergence follows from finite dimensional convergence, *cf.* [3], p. 19. □

Corollary 3.9. *For any sequence $\lambda_K = o(\log K)$,*

$$X_{\lambda_K} \underset{K\to\infty}{\overset{L^1}{\longrightarrow}} 0.$$

Proof. This is direct from

$$\mathbb{E}[X_{\lambda_K}] \le a^{\lambda_K - \log K} \to 0, \text{ as } K \to \infty. \qquad \square$$

This means that there is a very particular scale, $O(\log K)$, at which an interesting weak limit is obtained, whereas slower or faster rates result in simpler convergences, as exhibited.

4. Concluding remarks

Measuring population or set size in density rather than numbers, i.e. in capacity units, invites making the corresponding time change into an intrinsic scale also with unit K, $\bar{X}_t := X_{tK} = Z_{[tK]}/K, t \ge 0$. For that process Theorem 3.6 yields that

$$\bar{X}_0 \leftarrow \bar{X}_{(\log K)/K} = X_{\log K} \underset{K\to\infty}{\overset{D}{\longrightarrow}} h \circ W(z_0).$$

Thus, the process in the intrinsic time scale seems to have started from a random number of first elements, unless the variance of W is zero. Only in that case, corresponding to a completely deterministic initial reproduction or replication process, can the the number z_0 of ancestors or corresponding originators be recovered behind the random veil of history, by inversion of h [4].

As mentioned, this article was sparked by the concrete problem of finding the number of original templates in PCR and answering questions about single- or multicell origin of cancers.[7] It is, however, tempting to suspect that similar patterns of late observed growth with unknown, seemingly random, origin may occur in many other contexts.[9]

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